

# Matrix Population Models for Wildlife Conservation and Management

27 February - 5 March 2016

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## Lecture 6

### Time-Varying and Random environment Matrix models



Shripad TULJAPURKAR ("Tulja")  
who extensively developed the  
theory of population models in  
random environment

## When the model matrix varies from year to year....

### Time-Varying Models:

... in a known fashion over finite time window

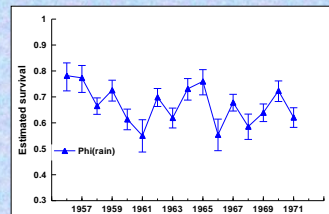
- Recorded sequence of bad and poor years
- Relationship between demographic parameter and env. covariate
- MAIN AIM: model a known trajectory (retrospective)

### Random Environment:

... in a random fashion over a finite or infinite time window

- Projection of relationship between parameter and env. covariate
- Unexplained year-to-year (environmental) variation
- MAIN AIM: projection, asymptotic behavior (prospective)

## Survival of storks in Baden-Württemberg estimated with rainfall in Sahel as a covariate



Model	(S <sub>r</sub> ,p)	(S <sub>rain</sub> ,p)	(S,p)
AIC	1349.50	<b>1339.15</b>	1356.10

$$\log(S / (1 - S)) = a + b \text{ rain}$$

## Storks in Baden-Württemberg: Modelling numbers with survival driven by rainfall in Sahel

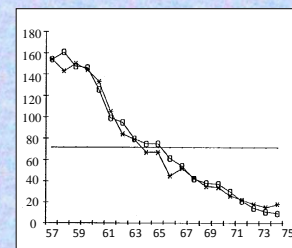
Year	57	58	...	i	i+1	...	74
Rain	$x_{57}$	$x_{58}$	...	$x_i$	$x_{i+1}$	...	$x_{75}$
Survival	$\phi_{57}$	$\phi_{58}$	...	$\phi_i$	$\phi_{i+1}$	...	$\phi_{75}$
Matrix	$M_{57}$	$M_{58}$	...	$M_i$	$M_{i+1}$	...	$M_{75}$

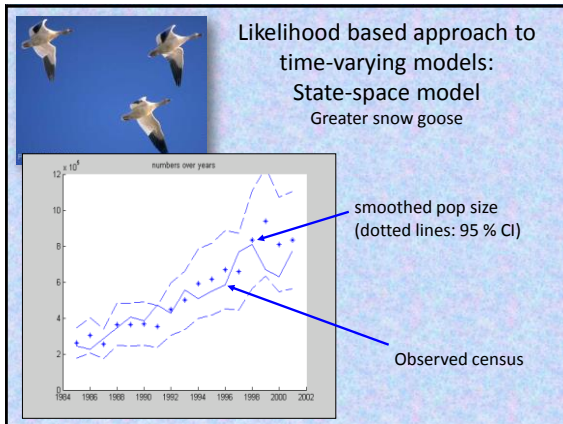
Numbers obtained by a « time-varying matrix model »  
(using  $N_{56}$  based on average stable age structure):

$$N_{i+1} = M_i \cdot N_i$$

## Storks in Baden-Württemberg: Modelling numbers with survival driven by rainfall in Sahel

An "ad hoc"  
comparison  
(o = model)  
(x = census)  
based on  
 $a_3 N_i(3) + N_i(4)$   
(Nr of breeders)





**Random Environment**  
 the scalar exponential model  
 (no stage/age classes)

$$n(t) = A_t n(t-1)$$

$A_t$  random scalar (i.i.d.), with  $E(A_t) = \lambda$

$$E(n(t) / n(t-1)) = \lambda$$

$$E(n(t) / n(0)) = \lambda^t$$

**Random environment**  
 Increasing variability

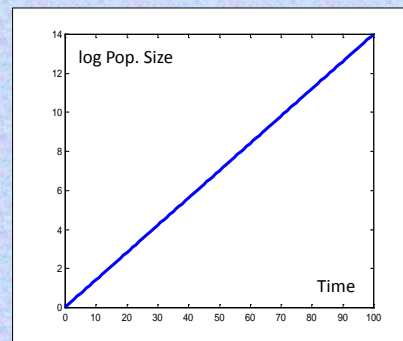
$$A_t = 1.15 \text{ with probability } 1 \Rightarrow \lambda = 1.15$$

$$A_t = 1.2 \text{ and } 1.1 \text{ with prob. } 0.5 \Rightarrow \lambda = 1.15$$

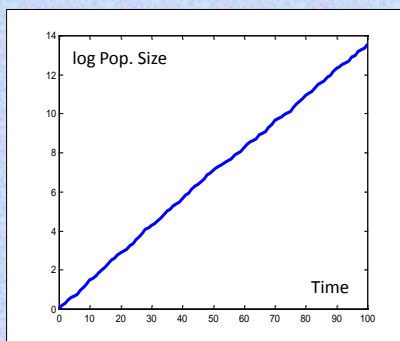
$$A_t = 1.4 \text{ and } 0.9 \text{ with prob. } 0.5 \Rightarrow \lambda = 1.15$$

$$A_t = 2.0 \text{ and } 0.3 \text{ with prob. } 0.5 \Rightarrow \lambda = 1.15$$

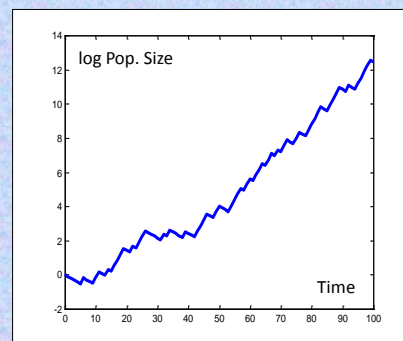
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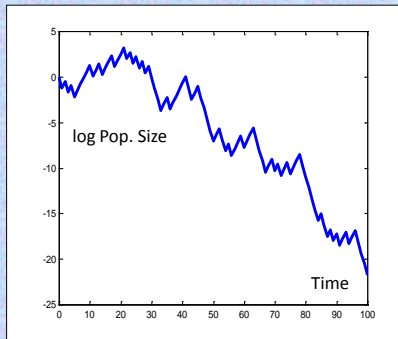
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$$A_t = 1.4 \text{ and } 0.9 \text{ with prob. } 0.5 \Rightarrow \lambda = 1.15$$



$A_i = 2.0$  and  $0.3$  with prob.  $0.5 \Rightarrow \lambda = 1.15$



### Where is the paradox ?

$$n(t) = A_t n(t-1) \Rightarrow n(t) = n(0) \prod A_i$$

$$\log n(t) - \log n(0) = \sum \log A_i$$

Central Limit Theorem:  $\sum \log A_i \approx \text{Normal distribution}$

$$\log n(t) - \log n(0) \approx \text{Normal}(\mu_t, \sigma_t^2)$$

$$a = E(\log A_i), v = \text{var}(\log A_i) \Rightarrow \mu_t = a t \quad \sigma_t^2 = v t$$

### The paradox is still there

$$\log n(t) - \log n(0) \approx \text{Normal}(\mu_t, \sigma_t^2)$$

$$\mu_t = a t, \sigma_t^2 = v t$$

$$\Rightarrow (\log n(t) - \log n(0))/t \approx \text{Normal}(a, v/t)$$

$$1/t \log n(t) \approx \text{Normal}(a, v/t)$$

$$v/t \rightarrow 0 \text{ when } t \rightarrow \infty \Rightarrow$$

$$1/t \log n(t) \rightarrow \log \lambda_s = E(\log A_i)$$

$$\text{However } 1/t \log E(n(t)) \rightarrow \log \lambda = \log E(A_i)$$

### Is the paradox still there ?

$A_i$ values	$\lambda$	EXPECTED	MOST PROBABLE
		$\log \lambda$	$\log \lambda_s$
1.15	1.15	0.1398	0.1398
1.2 1.1	1.15	0.1398	0.1388
1.4 0.9	1.15	0.1398	0.1156
2.0 0.3	1.15	0.1398	-0.2554

Most probable and expected trajectories differ

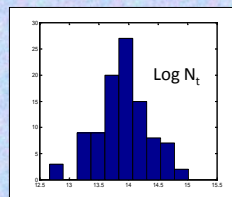
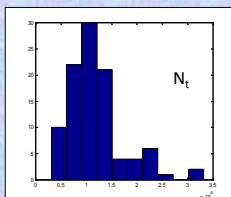


### There is no real paradox

$n(t) \rightarrow \text{log-normal distribution} \Rightarrow \text{Median} < \text{Expectation}$

$A_i = 1.2$  and  $1.1$  with prob.  $0.5$

Distribution for a large  $t$

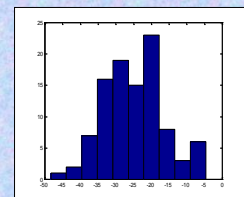
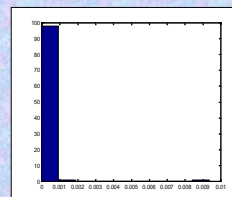


### There is no real paradox

$n(t) \rightarrow \text{log-normal distribution} \Rightarrow \text{Median} < \text{Expectation}$

$A_i = 2.0$  and  $0.3$  with prob.  $0.5$

Distribution for a large  $t$



## There is no real paradox

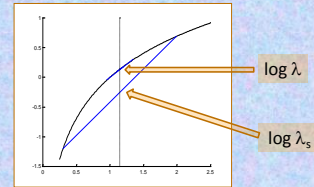
A few trajectories with large growth rate keep  
the expected growth rate equal to  $\log \lambda = \log E(A_t)$

Most probable trajectories are concentrated  
around  $\log \lambda_s = E(\log A_t)$  (more and more when  $t \rightarrow \infty$ )

*$\log \lambda_s$  is a relevant measure of growth rate*

## Environmental variability influences population growth

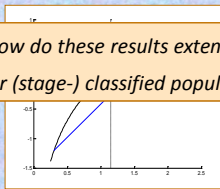
Jensen's inequality:  $\log \lambda_s = E(\log A_t) \leq \log \lambda = \log E(A_t)$



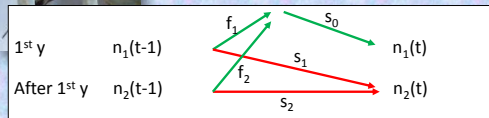
Environmental variability depresses Population growth  
A deterministically growing population may decrease

## The effect of Environmental variability on Population growth

*How do these results extend to  
age or (stage-) classified populations ?*



## The Barn Swallow example

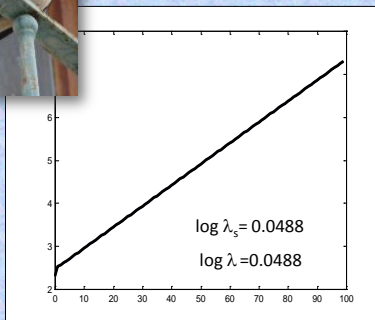


Average values  
 $s_0 = 0.2$   $f_1, f_2 = 3/2, 6/2$   
 $s_1 = 0.5$   $s_2 = 0.65$

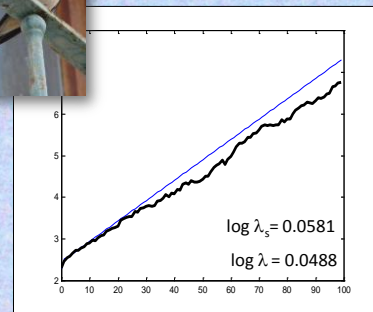
$$A = \begin{pmatrix} f_1 s_0 & f_2 s_0 \\ s_1 & s_2 \end{pmatrix}$$

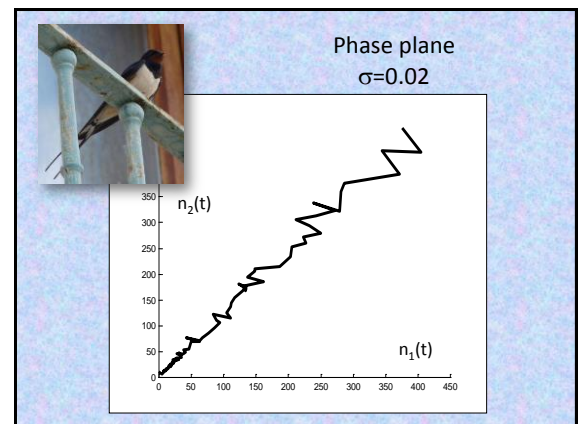
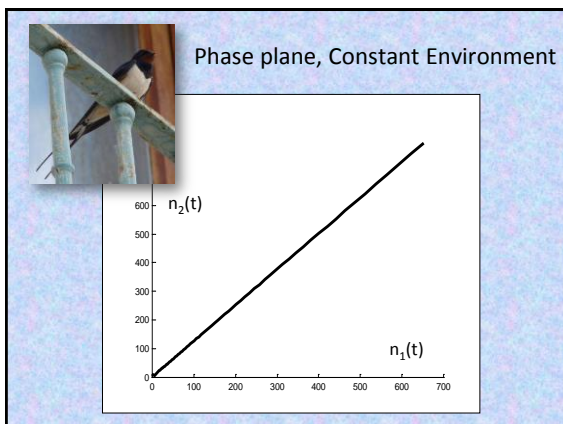
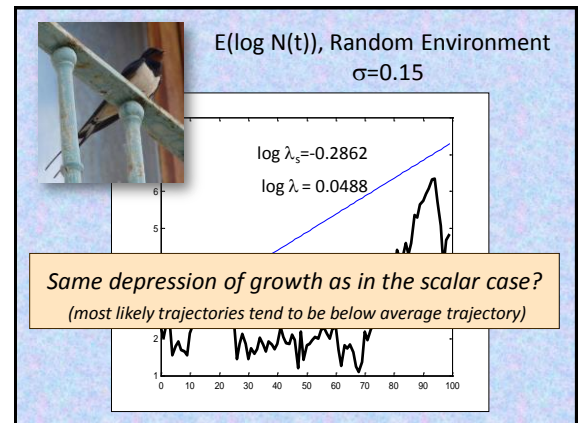
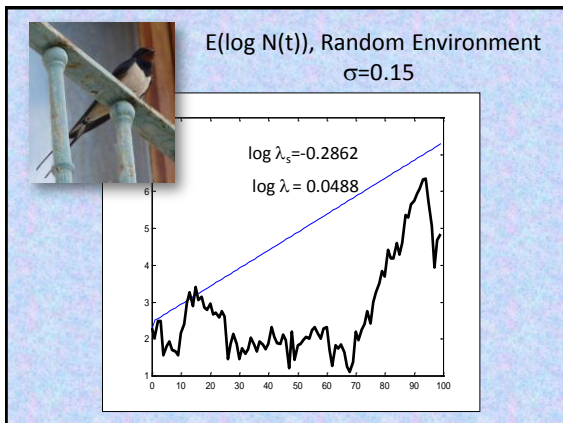
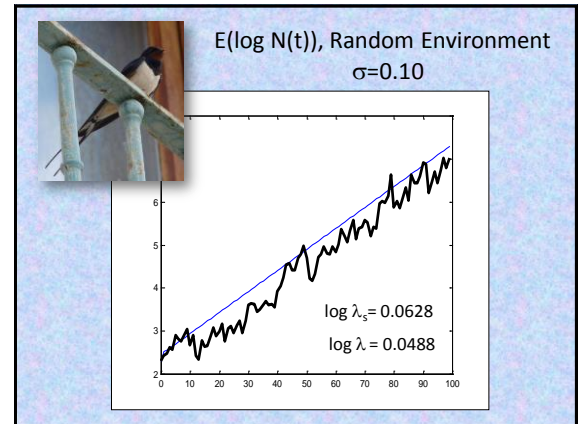
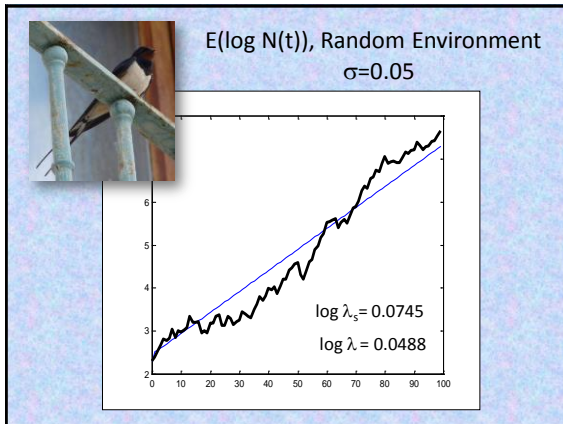
*+ random Survival with variance  $\sigma^2$*

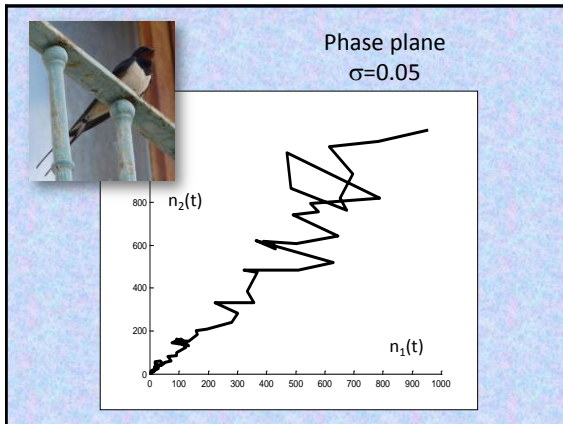
## $E(\log N(t))$ , Constant Environment



## $E(\log N(t))$ , Random Environment $\sigma=0.02$







Same depression as above ...plus a constant mismatch in age structure

$$\log \lambda_s \neq \log(E(A_t)) = \log \lambda$$

$$\log \lambda_s \neq E(\log(A_t)), A_t \text{ being a matrix}$$

$$\log \lambda_s \neq \log E(\lambda(A_t)), n_t \neq \text{eigenvector of } A$$

Convergence of  $1/t \log c' n(t)$  to  $\log \lambda_s$   
even under correlated environments

("Ergodic theorems on products of random matrices")

How to calculate the asymptotic growth rate ?

"The computation is considerably more involved than in the scalar case" S.Tuljapourkar (1990)



Simulation or Approximation

Estimation of  $\log \lambda_s$   
Simulation and approximation

Simulation: Matlab, ULM.

Large number of repetitions needed

Approximation : valid from small variability

For uncorrelated parameters:

$$\log \lambda_s \approx \log \lambda - \frac{1}{2\lambda^2} \sum \left( \frac{\partial \lambda}{\partial \theta} \right)^2 \text{var}(\theta)$$

Estimation of  $\log \lambda_s$   
Approximation

$\sigma$	$\lambda$	APPROXIMATE	
		$\log \lambda$	$\log \lambda_s$
0.00	1.05	0.0488	0.0488
0.01	1.05	0.0488	0.0486
0.05	1.05	0.0488	0.0442
0.10	1.05	0.0488	0.0304
0.15	1.05	0.0488	0.0075
0.20	1.05	0.0488	-0.0246

Random Environment simulation in ULM

In batch file (or using interpreted command "changevar"),  
Just define the parameter of interest as random.

Several continuous distributions are available.

The parameter value will be evaluated at each time step.

"0.1+rand(0.2)"  $\iff$  0.1+Unif[0, 0.2]  $\iff$  Unif[0.1, 0.3]

Fixed environment

{ juvenile survival rate  
defvar s0 = 0.2

{ subadult survival rate  
defvar s = 0.35

{ adult survival rate  
defvar v = 0.5

Random Environment

{ juvenile survival rate  
defvar s0 = 0.1+rand(0.2)

{ subadult survival rate  
defvar s = 0.35

{ adult survival rate  
defvar v = 0.5

